Pedobiologia 39, 97–106 (1995)
Gustav Fischer Verlag Jena

Autecological study of some earthworm species (Oligochaeta) by means of ecological profiles

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Summary. An autecological study was carried out in Asturias, León, Zamora and Salamanca (Spain) and the ecological characteristics of twelve species of earthworms (one with two subspecies) were analysed by construction of ecological profiles, a technique relating the species' occurrences to selected ecological factors by dividing each factor's range of values into classes. This is a different approach to the many ecological studies that have considered the earthworm community and not the species individually.
The main factors influencing distribution for the majority of earthworm species were pH, calcium, magnesium, aluminium, C/N ratio and organic matter levels.

Key words: Earthworms, ecological profiles, Spain

Introduction

The term "ecological profile" was introduced by Gounot (1958) to describe the distribution of a species in relation to environmental variables, expressed as the frequency of occurrence over a series of class intervals. Later, Godron (1964) established differences between several kinds of ecological profiles. Since then this technique has been employed in several autecological studies, almost exclusively floristic, and has been developed by the French School, most notably Godron et al. (1968) and Guillerm (1971).
There are very few faunistic studies which use this technique. However, we believe that, to date, it is one of the most suitable in terms of determining the individual relationships of species to the factors under study as it avoids the assumption, common in other types of numerical techniques such as regression or correlation, of a linear response of the species to the factors. In nature, species respond according to a Gaussian model where numbers are concentrated at certain intervals, decreasing away from the optimum value of the resource, according to the organism's level of tolerance.
Canonical correspondence analysis (ter Braak 1986) allows a direct relationship between species and factors and extracts the most influential factors acting upon the community but the individual response of some species can be diluted.

Materials and Methods

Sampling was carried out in 63 localities in Asturias, León, Zamora and Salamanca (Spain) whose location and characteristics are shown in Briones et al. (1991). Three biotopes (meadow, river bank and woodland) were considered in each locality, resulting in 189 samples in total.

Earthworms were captured by the formalin-hand sorting method (Bouché 1972) over 1 m^2. The specimens were fixed in a 1 : 1 solution of alcohol-formalin, consisting of 96% alcohol and 10% formalin, and were later preserved in 10% formalin.

Three soil samples, one in each biotope, were collected before spreading the formalin, and twenty soil factors were measured: moisture (HUM) (Min. = 6.27, Max. = 77.19), porosity (POR) (Min. = 37.26, Max. = 96.42), aeration (AIR) (Min. = 6.28, Max. = 77.82), gravel (MM2) (Min. = 0.21, Max. = 77.56), coarse sand (GRU) (Min. = 1.31, Max. = 83.28), fine sand (FIN) (Min. = 2.50, Max. = 64.33), coarse silt (LIG) (Min. = 0.05, Max. = 40.94), fine silt (LIF) (Min. = 1.00, Max. = 63.78) and clay (ARC) (Min. = 0.57, Max. = 50.90) as percentages, pH in distilled water (PHH) (Min. = 3.80, Max. = 8.60), pH in potassium chloride (PHK) (Min. = 2.70, Max. = 8.30) and pH of the litter (PHV) (Min. = 3.90, Max. = 8.90), according to the method proposed by Guitián & Carballas (1976). Carbon (C) (Min. = 0.12, Max. = 13.82), nitrogen (N) (Min. = 0.02, Max. = 1.20), as percentages and sodium (Na) (Min. = 0, Max. = 6.53), potassium (K) (Min. = 0.01, Max. = 3.24), calcium (Ca) (Min. = 0.21, Max. = 49.0), magnesium (Mg) (Min. = 0.01, Max. = 18.15) and aluminium (Al) (Min. = 0, Max. = 11.23) were estimated as meq/100 g, according to Anonymous (1982). The C/N ratio was also calculated (Min. = 0.73, Max. = 20.43).

The individual response of each species was investigated by means of ecological profiles, a technique that allows the researcher to study the relationship of every single species to each factor, dividing the factor range into classes. Class intervals were determined by noting inflexion points on cumulative frequency curves according to Daget & Godron (1982). Thus, class intervals were obtained for the twenty edaphic factors and once established were tested against every single species, changing the number of occurrences in each class interval when a new, different species was taken into consideration. We also included an additional factor, the biotope (meadow = ●, river bank = ○ and woodland = □) because we believe that it could have some influence on the ecological behaviour of all species, beyond that of the selected properties that have been measured.

The number of class intervals ranged between three (aluminium) and six (porosity), being the majority with five classes.

The profile using the absolute frequencies shows the number of samples where a species was present. The profile of relative frequencies shows the number of samples with the species considered in relation to the total number of samples in each class interval of the factor.

Usually, the samples are not uniformly distributed in the ecological profile and irregularities are frequent. To avoid this, the profile using the corrected frequencies is elaborated according to the formula:

$$C(K) = \frac{U(K)/R(K)}{U(E)/NR}$$

C(K) = Corrected frequency of the single species E in the factor class K, *U(K)* = Occurrences of the species E in the factor class K, *U(E)* = Total number of occurrences of the species E, *R(K)* = Number of samples in the factor class K, *NR* = Total number of samples

The natural logarithm of these corrected frequencies has been used because graphs constructed directly from the corrected frequencies tend to overvalue the factor classes with a positive action upon species relative to those with a negative effect.

In this way, corrected frequency values with the same intensity but opposite sign are symmetrical (Romero & Fraga 1990). The classes with frequencies equal to zero (Ln0 = -infinity) are shown with an arrow at the end of the column. Moreover, the factor entropy value and the mutual species-factor information were calculated for each factor in order to obtain the information value of each ecological factor, according to the following formulae:

$$H(L) = \sum \frac{R(K)}{NR} \log_2 \frac{NR}{R(K)}$$

$$I(L, E) = \sum \frac{U(K)}{NR} \log_2 \frac{U(K)}{R(K)} \frac{NR}{U(E)} + \sum \frac{V(K)}{NR} \log_2 \frac{V(K)}{R(K)} \frac{NR}{V(E)}$$

H(L) = Entropy value of the factor L, *R(K)* = Number of samples in the factor class K, *I(L, E)* = Mutual information of the species E and the factor L, *U(E)* = Total number of occurrences of the species E, *V(E)* = Total number of absences of the species E, *V(K)* = Number of samples of the factor class K in which the species E is not present, *U(K)* = Occurrences of the species E in the factor class K, *R(K)* = Number of samples in the factor class K, *NR* = Total number of samples.

Species present in every sample will provide reduced information and the minimum value will be obtained when the species' occurrences are equitably distributed in every samples, i.e. species are not affected by this factor.
The entropy factor value and the mutual species-factor information are represented on a Cartesian axis according to Godron et al. (1968). The factors with a greater value of mutual species-factor information will be the "effective" ones (Daget & Godron 1982). Drawing a bisectrix to both axes, the effective factors will be the most distant from this bisectrix to its upper part.

Results

Only 12 species out of 33 collected in the quantitative samplings occurred at more than 10% of the sampled sites, and only these were considered for analysis: *Allolobophora caliginosa caliginosa* (Savigny 1826) (AC), *A. c. trapezoides* (Dugès 1828) (AT), *A. chlorotica* (Savigny 1826) (AH), *A. rosea* (Savigny 1826) (AR), *Dendrobaena madeirensis* Michaelsen 1891 (DD), *D. mammalis* (Savigny 1826) (DM), *D. rubida* (Savigny 1826) (DR), *Eisenia eiseni* (Levinsen 1884) (EE), *Eiseniella tetraedra* (Savigny 1826) (ET), *Lumbricus rubellus* Hoffmeister 1843 (LR), *L. friendi* Cognetti 1904 (LF), *Octolasion cyaneum* (Savigny 1826) (OY) and *O. lacteum* (Öerley 1881) (OL). As a consequence of this restriction there were no records from four localities; thus, we worked with the 185 remaining sites.
Fig. 1 displays the ecological profiles of *Dendrobaena madeirensis*. The positive values indicate a positive action of the factor upon this species and the negative values the opposite action. From this graph it can be seen that the distribution of this species seems to be related to high values of moisture, porosity, aeration, fine silt, carbon, nitrogen and aluminium, or in other words it avoids low values of the above factors and prefers the low values of calcium, magnesium and pH. For the remaining factors it either prefers the average values or does not show a clear tendency. With respect to the biotope, it is a species that lives in meadows (M) and woodlands (W).
Fig. 2 shows the effective factors calculated using the average value of the mutual species-factor information of the twelve species considered. They are, in this order: biotope, calcium, pH in distilled water, pH of the litter and aluminium.
In order to obtain a more individual characterization, the effective factors for each species were calculated, so that one could tell whether a factor is effective for one species but not for all. The results are displayed in Table 1, where it can be seen that for the majority of the species pH, exchangeable cations and texture can explain their presence in a certain habitat. But there are some differences, even in species sharing the same environment like those of the *Allolobophora* genus, in which factors play an important role in the distribution of these species.
Besides the factors mentioned above, distribution of *A. rosea* (AR), *D. rubida* (DR) and *E. tetraedra* (ET) is strongly influenced by the biotope although *L. friendi* (LF) and *O. cyaneum* (OY) seem also to be influenced. Nitrogen content is an important factor for *L. friendi* (LF) and *O. cyaneum* (OY), the latter also being related to organic matter content, whereas for *A. chlorotica* (AH) nitrogen has less importance. Porosity affects the distribution of *A. c. caliginosa* (AC) and *D. madeirensis* (DD), aeration that of *A. c. trapezoides* (AT) and *A. rosea* (AR), gravel that of *A. chlorotica* (AH) and *A. rosea* (AR), moisture that of *E. tetraedra* (ET) and *L. rubellus* (LR) and C/N ratio that of *A. c. caliginosa* (AC), *D. mammalis* (DM) and *L. rubellus* (LR).
In Fig. 3 the results of ecological profiles for all species considered are shown. The shaded areas indicate preferences towards low, medium or high values of the factor studied. No preference towards any value is shown by discontinuous shading. Moreover, the biotope in which the species was captured in abundance is given. In addition the statistically significant relationships of each species to edaphic factors are shown, as demonstrated by

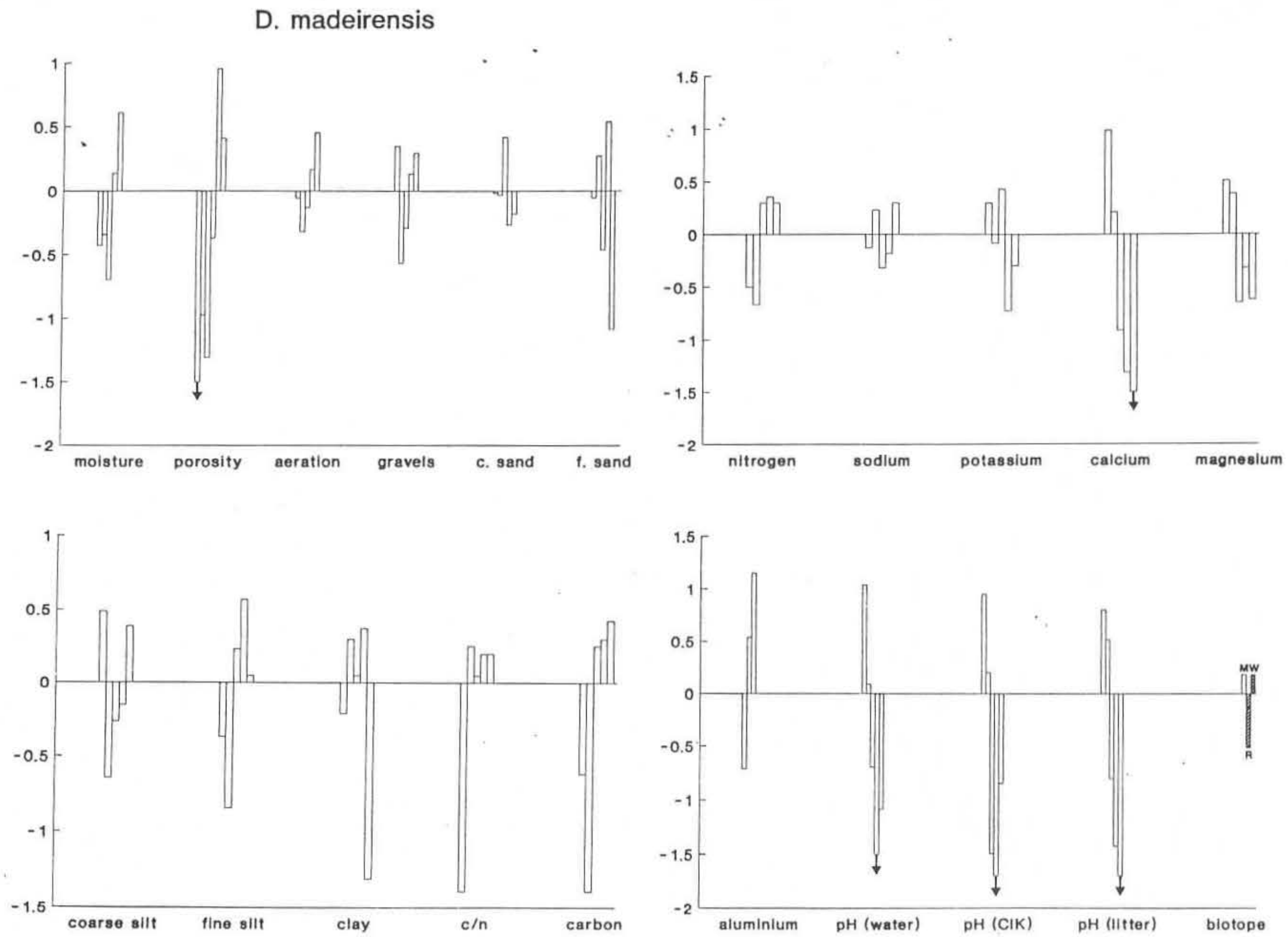

Fig. 1. Ecological profiles of *Dendrobaena madeirensis* using the natural logarithm of the corrected frequencies. The arrow at the end of the column shows classes with frequencies equal to zero (Ln0 = -infinity). Biotope: M = meadow, R = river bank, W = woodland

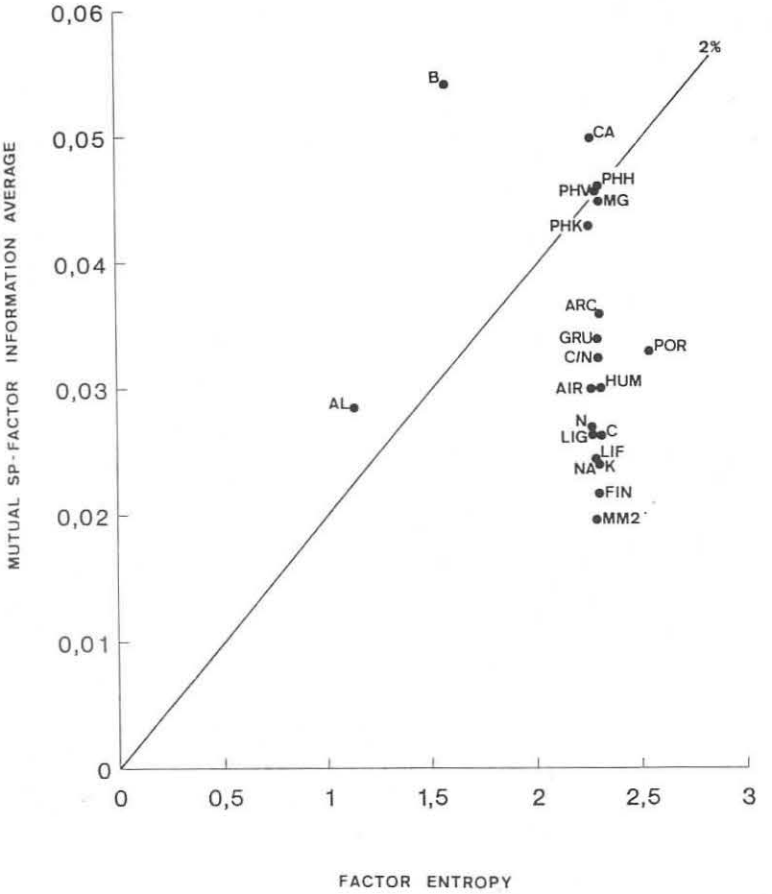

Fig. 2. Effective factors: the average value of the mutual species-factor information for the twelve species considered is represented against the factor entropy value (abbreviations in the text)

Table 1. Effective factors for each species in decreasing order of effectiveness

Effective Factors

Earthworm species

AC	AT	AH	AR	DD	DM	DR	EE	ET	LF	LR	OY	OL	Effectiveness
Ca	Mg	PHK	B	PHH	ARC	B	Mg	B	N	PHV	ARC	Ca	
PHH	AIR	PHH	AIR	PHK	C/N	K	PHH	HUM	ARC	PHK	N	Na	
Mg	PHV	PHV	GRU	Ca	Ca	LIF	PHK		LIF	PHH	C		
C/N	Al	Ca	Mg	POR	Al	LIG	Al		B	HUM	B		
K		Al	LIG	PHV		Mg	Ca			C/N			
POR		N	Ca	Al			PHV			Ca			
PHK		FIN	MM2							FIN			
ARC		MM2	ARC							Al			
			Al										

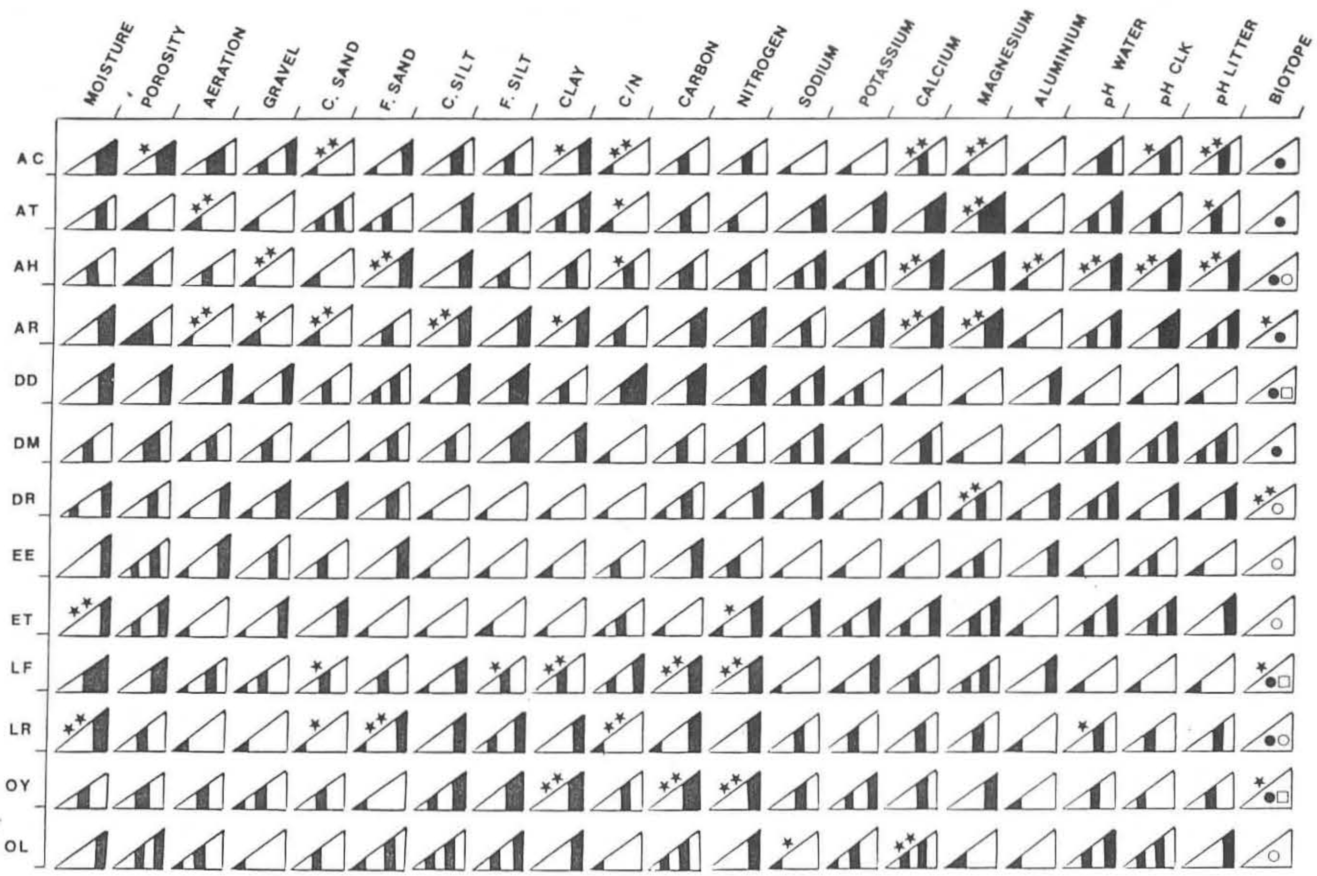

Fig. 3. Results of ecological profiles for the twelve species considered. The shaded areas indicate preferences towards low ( ), medium ( ) or high values ( ) of the factor studied. Biotope: ● = meadow, ○ = river bank, □ = woodland. Significance was calculated by means of a χ^2 calculation of the homogeneity of both expected and observed occurrences and absences ("index profile"), and is denoted by either one or two asterisks when $p < 0.05$ or 0.01, respectively

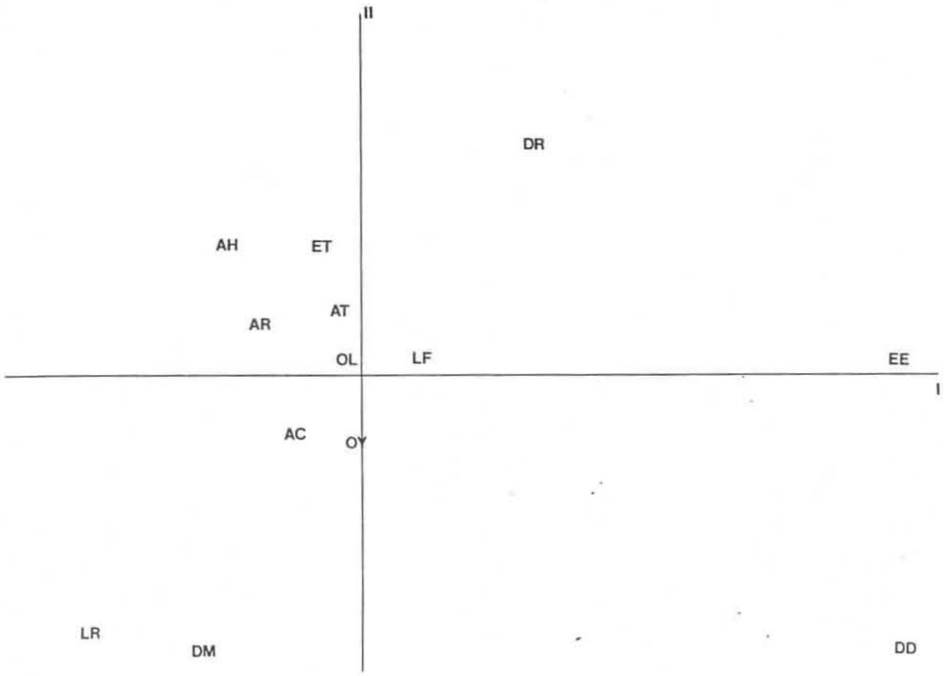

Fig. 4. Correspondence analysis of ecological profiles. Results for the first two axes. Species (abbreviations in the text)

the application of ecological profiles. Significance was calculated by means of the "index profile", a χ^2 calculation of the homogeneity of both expected and observed occurrences and absences, and is denoted by either one or two asterisks when $p < 0.05$ or 0.01, respectively.

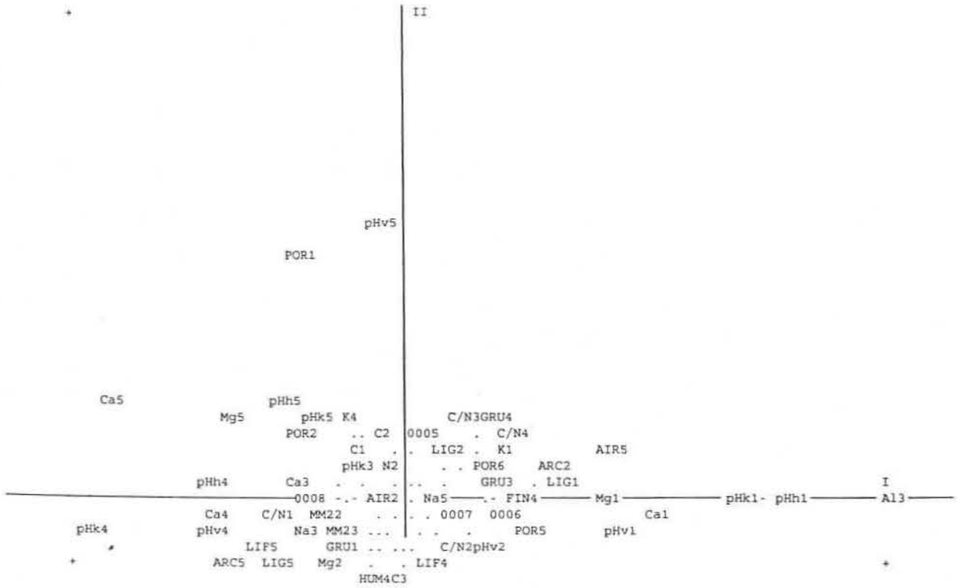

Fig. 5. Correspondence analysis of ecological profiles. Results for the first two axes. Intervals of factors expressed as the factor symbol followed by the number of class

As it can be seen in Fig. 3, for some species, such as *D. madeirensis* (DD), *D. mammalis* (DM), *D. rubida* (DR) and *E. eiseni* (EE) (almost all factors) and *L. rubellus* (LR) (some factors), it was impossible to calculate the significance because of their limited occurrence (these species are at the limit of the 10% pre-established restraint).

To summarize the information obtained from the ecological profile analysis in a different way, a multifactorial correspondence analysis using species data and the class intervals of soil factors was carried out, according to Galindo et al. (1986). Each class interval is expressed as the factor symbol followed by the number of the class, five for the majority of the factors, three for aluminium and six for porosity. This allowed us to see ecological groups as a function of the variables measured. The results are shown in Fig. 4 and Fig. 5. In order to avoid the overlapping of factor labels the factor graph scale has been extended, so the positions of the labels are relative and it cannot be directly superimposed on the species graph, but conclusions can be drawn.

Axis I separates, towards its positive side, acid sandy soils (A13, GRU4) with high porosity (POR5, POR6) and high C/N ratio (C/N4) characterizing *D. madeirensis* (DD), *E. eiseni* (EE) and *D. rubida* (DR) from less acid (pHk4, pHh4, pHv4, Ca5, Ca4), clayey-silty soils (LIF5, LIG5, ARC5) associated with *A. chlorotica* (AH), *A. rosea* (AR), *L. rubellus* (LR) and *D. mammalis* (DM). *E. tetraedra* (ET), *A. c. trapezoides* (AT), *A. c. caliginosa* (AC), *O. lacteum* (OL), *L. friendi* (LF) and *O. cyaneum* (OY) are not clearly defined. Axis II proved to be less interpretable.

In this paper we did not follow the second option of Galindo et al. (1986) in carrying out a new analysis, regrouping the data and establishing only three classes for every factor, in order to obtain more representative values. Three classes is a very low number, and our objective was to compare the results of this analysis with those obtained by means of ecological profiles.

Discussion

The study of the relationships between earthworms and soil factors is difficult because of the great complexity of the environment in which they live, which is the result of the interaction of biotic and abiotic variables that are difficult to measure and are generally very variable.

There are a number of papers that have tried to approach this subject from one or both of two points of view; on the one hand, the individual relationship of each species to each factor (linear regression, U of Mann-Whitney), and on the other hand, the whole relationship of each species to all of the factors as a group presented in interaction (multiple regression, canonical correlation, correspondence analysis, principal components and canonical correspondence analysis). These two approaches are often combined, making the analysis more complicated.

In an autecological study, such as the present one, the influence of soil factors on each species individually can be seen, and the tendencies of the species' occurrences over the measured range. However, in this kind of study the range of variation comes directly from the variability of the zone under study so the conclusions cannot be extrapolated to another zone.

The final result from the whole study, taking all of the species with all of the factors, is to isolate those factors that have a major influence on the community, so that it is the one that answers to the interacting environmental conditions rather than the single species. One factor may or may not be suitable for an individual species but its effect is diluted in favour of the dominant one when the community is considered.

Thus, for example, one species may be favoured by high moisture, fine texture, abundant organic matter, acid soils and abundant plant cover but may survive in environments with coarse textures and limited amount of plant cover if the pH is low, although its relative abundance could be considerably lower than under optimal soil conditions. The main factor is pH compared to the other factors which are secondary in importance.

In comparison with previous work applying detrended canonical correspondence analysis to the same data (Briones et al. 1992), it can be seen that only the autecological view can obtain information on the influency of certain factors on a single species that are not preponderant for the community such as moisture, porosity, aeration, texture and biotope.
In spite of that, both types of study are important and complementary for broadening our present knowledge of the ecology of earthworms. A synecological study allows us to extract the factors having the most influence on community structure and to identify species groups with a similar response. An autecological study allows us to determine the factors that condition the presence and the abundance of single species.
Such studies can provide a useful basis for laboratory and field experiments, including assessing optimal conditions for earthworm culture. Finally, these studies can also detect differences in ecological features between races, subspecies and varieties, and may even enable us to characterize ecotypes that are impossible to separate on anatomical characters.
In the literature, the different kinds of studies described here are often mixed together, and the problem arises that the results obtained using different numerical techniques cannot be compared when the objectives are different. Other difficulties come from errors in measurement, type of data, species under study, etc., according to Mascato et al. (1987).
There is very little research that has used autecological data processing. For some authors autecology consists of drawing up a list of data on soils from which the species were collected without doing any numerical processing that would shed light on the significance of the conclusions. Other authors establish species classifications according to the species' ecological ranges, but as in the former case, they give no statistical analysis.
Amongst few comparable studies, Satchell (1955) and Nordström & Rundgren (1974) employing linear regression, Calvín & Díaz Cosín (1985) using the Student t, Mariño et al. (1985) and Mato et al. (1986) using U of Mann-Whitney and Mascato et al. (1987) and Trigo et al. (1989) using ecological profiles, obtained similar results except for some contradictions due to a superposition of interval values for the factors measured. Each paper brings forward new information on the environmental characteristics of some species not studied previously. Our research combines the distribution of all species studied in relation to twenty edaphic factors and plant cover using an autecological method that allows evaluation of every species individually.
In short, after combining the information extracted from previous papers with our own results, we may conclude that the factors which establish differences in the ecological behaviour of earthworms are pH, organic matter and some exchangeable cations, mainly calcium, aluminium and to a lesser extent, magnesium.

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